BOOK REVIEW

doi:10.1111/evo.13

SSE SOCIETY for the STUDY of EVOLUTION

EVOLUTION INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

Book review of Prum, R. O. 2018. *The evolution of beauty: How Darwin's forgotten theory of mate choice shapes the animal world—and us (2017)*, Doubleday, 428 pages, ISBN: 9780385537216

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Received October 8, 2018
Accepted October 9, 2018

We were eager to read Richard Prum's recent book, *The Evolution of Beauty: How Darwin's Forgotten Theory of Mate Choice Shapes the Animal World—and Us* (2017). As behavioral ecologists and evolutionary biologists studying animal mating behavior and communication, we appreciated the book's focus on the aesthetics of mate choice, its engaging descriptions of the natural world, and its representation of a diverse group of scientists and their research. The book is beautifully written and accessible to nonscientists, and we recognize its value in engaging the public in the study of evolution. We disagree, however, with the book's advocacy of a single evolutionary explanation for beauty in nature, and we were disappointed by its portrayal of modern sexual selection research, which was strikingly out of step with our own research programs and those of our colleagues.

The central argument of the book is that evolutionary biologists have dismissed "Darwin's *really* dangerous idea" (Prum 2012): that the subjective, aesthetic experiences of (female) animals are key to explaining the evolution of "beauty." These ideas were originally proposed in a series of papers on aesthetic evolution (Prum 2010, 2012). In these articles, beauty was equated with the Fisherian model of coevolution, whereby secondary sexual traits become exaggerated solely as a byproduct of genetic covariation between "desire" (female preference) and "ornament" (male display) (Fisher 1930; Lande 1981; Kirkpatrick 1982). Renamed the "Beauty Happens" hypothesis for the book, Fisherian coevolution can lead to the exaggeration of sexual ornaments via a positive feedback process in which preferences that have no survival or fecundity benefits for females are selected indirectly, through genetic correlation with the preferred ornaments. Beauty Happens is explicitly contrasted with adaptive mate choice, where male displays serve as indicators of either direct benefits, such as high-quality territories or nuptial gifts, or genetic benefits, such as genes for immune function or metabolic health that could be inherited by offspring (i.e., "good genes"). With adaptive mate choice, mate preferences evolve because of these direct or genetic fitness benefits to choosy females.

We agree that mate choice for indicators is often assumed as an explanation for the evolution of elaborate displays without sufficient consideration of other processes; however, we share many of the same concerns expressed in other critical reviews of the book, such as Borgia and Ball (2018) and Kempenaers (2017). Here, we first describe our concerns with the book's treatment of central concepts like beauty, desire, aesthetics, and sexual selection. We then discuss problems with its main assertion that Fisherian selection is a null model of intersexual selection, and we highlight numerous alternative hypotheses for display evolution

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that are either dismissed or ignored. Finally, we take issue with the book's argument that the behavior of female (nonhuman) animals should serve as a moral compass for our own behavior.

A PROBLEMATIC FRAMEWORK

One of the book's greatest strengths is that it forces us to confront potentially thorny but fundamentally important concepts like "beauty," "desire," and "aesthetics," discussed in turn below. Modern evolutionary biologists tend to avoid these terms and concepts for fear of anthropomorphism, but the book confronts them head-on, highlighting a number of areas where future research may be fruitful. Unfortunately, that confrontation is clouded by vague definitions and inconsistent use of terms. More importantly, by narrowly defining these concepts as the causes and effects of Fisherian coevolution, the book dismisses alternative explanations and constrains the phenomena we aim to understand to a particular worldview.

Beauty, for example, is defined as "the result of a coevolutionary dance between desire and display" (p334). This is problematic for at least two reasons. First, according to this definition, nearly everything we consider beautiful—wildflowers, rainbows, manakins, mountain meadows—is excluded from consideration, simply because our own aesthetic preferences cannot have coevolved, in a Fisherian process or otherwise, with flowers or mountain meadows.

Although early in the book, readers are warned that the beauty examined here is not what humans experience but rather what nonhuman animals (i.e., the target receivers of beautiful displays, specifically, birds) experience, it bears noting that the examples of beauty in the book, from peacocks to manakins, are also beautiful to people. Readers therefore could not be blamed for assuming, as we did initially, a broader definition of beauty. Rather, what the book appears to try to explain is the evolution of exaggerated secondary sexual traits exhibited by males of many bird species (hereafter "displays," to encompass both static and dynamic aspects of courtship behavior). Though we are equally curious as to why people find flowers, waterfalls, and sunsets beautiful, we restrict the focus of our review on what we take to be the book's central argument: that the Fisherian coevolutionary process is ubiquitous and should be the null model explaining the evolution of animal sexual displays.

More importantly, a definition of beauty that excludes alternative explanations is surely not a productive starting point for advancing our understanding of the natural world. Productive science identifies and quantifies a phenomenon in need of explanation and proposes multiple alternative hypotheses with unique predictions. If beauty is the phenomenon to be explained, then it cannot be defined as the result of a candidate hypothesis. This definition excludes noncoevolutionary hypotheses, discussed below, and while the book acknowledges that indicator processes may fall under the definition, "beauty" and "adaptive value" are treated as incompatible through much of the book.

Another problematic concept in the book is desire. Female desire is presented as the driving force for the evolution of male sexual displays, which is hardly controversial. What is frustrating, however, is the lack of an explicit *definition* of desire, at least for the purposes of argument and clarification. Prum justifiably insists that "the study of aesthetic evolution requires engaging with both . . . the object of desire and the form of desire itself (p8)," yet the book offers no thoughtful exploration of desire beyond the human female orgasm (chapter 9). Fitting together passages throughout the book, it would be fair to conclude that desire is sexual, subjective, irrational, unpredictable, and autonomous, but we find no passage in which it is explicitly defined. This is an unfortunate oversight, because psychologists are carefully exploring the concept of desire—distinguishing liking (the hedonic experience) from wanting (incentive salience) at the neurological level, for example (e.g., Berridge et al. 2009). Simultaneously, evolutionary biologists are applying these advances to animal decisions (see Rosenthal 2017 and Ryan 2018). A distinction between liking and wanting is especially relevant to the ideas presented in this book. If an appreciation of beauty is a form of liking and sexual desire is a form of wanting, for example, then the "beauty happens" hypothesis appears to conflate them, though they are clearly distinguishable. Flower color patterns are attractive to pollinating insects, but pollinators do not attempt to copulate with them (with the notable exception of deceptive flowers, like "bee orchids," that mimic female pollinators). Aposematic patterns are beautiful (at least to us) but not sexually desired; and human penises (chapter 8) are sexually desired but arguably not beautiful (but see Mautz et al. 2013). The book's definition of beauty appears to view desire as sexual motivation resulting from a Fisherian process of mate choice, thus either negating a potential role of "liking" in mate attraction, or conflating liking and wanting. Again, the book constrains the definitions of phenomena we aim to understand.

Intimately related to the concept of desire is that of aesthetics. Defining aesthetics is a challenging task but an essential one, given its central status in the book. Here, we are given more guidance: "I call the evolutionary processes that are driven by the sensory judgments and cognitive choices of individual organisms aesthetic evolution (p8)." Yet, unlike other narrow definitions discussed previously, this is clearly too broad a definition. If aesthetics are the sensory judgments and cognitive choices underlying animal decisions, then all of animal behavior is aesthetics (see Mendelson et al. 2016). However, by piecing together various passages throughout the book, aesthetics appears to be more narrowly restricted to those judgments and choices that cause pleasure (p.272; Chapter 9). While a link between aesthetics and pleasure is often invoked in philosophy (e.g., Zangwill 2014), addressing this link biologically, and testing its role in evolutionary processes, requires an explicitly proximate perspective. That proximate perspective is frustratingly lacking in most of the book. Fundamental questions about potentially distinct mechanisms of pleasure (e.g., sexual or nonsexual? sensory or cognitive? tactile or visual?), or proximate mechanisms of desire or preference, are not only unanswered but unasked.

In contrast to their portrayal in the book, animal behaviorists have been addressing the role of the subjective experience in evolution since Von Uexküll's foundational call to consider the *Umwelt* (i.e., sensory world) of organisms (Von Uexküll 1934); though they have favored less anthropomorphic terms like "receiver psychology" and "reward." Guilford and Dawkins' paradigm-shifting argument for a role of the "psychological landscape" in signal evolution was strikingly similar to Prum's broader view of aesthetics (Guilford and Dawkins 1991; also see Rowe 2013). Two new books by Rosenthal (2017) and Ryan (2018) carefully consider the subjective sensory and cognitive experience of the receiver in mate choice, and multiple reviews have done the same for animal communication more broadly, including mate choice and other signaling contexts, such as social and antipredator signaling (Jennions and Petrie 1997; Bradbury and Vehrencamp 1998; Endler and Basolo 1998; Rowe 1999; Patricelli et al. 2003; Hebets and Papaj, 2005; Bateson and Healy 2005; Miller and Bee 2012; Ryan and Cummings 2013; Patricelli and Hebets 2016; Mendelson et al. 2016). Indeed, in our opinion, the most exciting research in sexual selection and animal communication over the last few decades has been in addressing the sensory judgments and cognitive choices of receivers. Thus, while perhaps emphasizing pleasure more explicitly, the core ideas in the book are not as revolutionary as they are claimed to be (p25); rather, they add to large body of literature exploring the subjective experience of mate choice and its role in behavioral evolution.

The villain in this tale is adaptive mate choice (AMC), defined broadly as mate choice that provides a "better fit between the organism and its environment (p298)," and more specifically throughout as a choice that increases the survival or fecundity (hereafter, "viability") of the chooser or its offspring. Also known as the indicator model of sexual selection, AMC is portrayed as the orthodoxy—a cold-hearted, joylessly utilitarian, pan-adaptationist, eugenic approach that Prum aims to overthrow. AMC is contrasted with Fisherian mate choice that is independent of, or even detrimental to, the viability of the receiver or her offspring. Consistent with the sexual selection literature, the latter is termed "arbitrary" (i.e., displays are arbitrary with respect to viability). Mate choice that is both arbitrary and aesthetic forms the foundation of the Beauty Happens hypothesis.

The first problem here is the contention that arbitrary and aesthetic mate choice has become a "Forgotten Theory" (as the title of the book claims) as researchers embrace the AMC. We are active researchers in an active field, and we can attest that neither we nor many of our colleagues discount the possibility that mate choice can be neutral or detrimental to a receiver's viability. Indeed, Lande (1981), which provides a quantitative genetic model for Fisherian selection, is the most highly cited model of speciation by sexual selection (Fitzpatrick et al. 2018), suggesting that most researchers identify viability-neutral mate choice as a feasible model for the diversification of sexual displays. This "forgotten" theory is in fact covered prominently in every modern textbook that discusses sexual selection.

The second problem is characterizing the field as entirely accepting of the "orthodox" view of indicator models. We do not discount Prum's experiences with manuscript reviewers or colleagues that promote adaptive mate choice. Moreover, we agree that indicator thinking is pervasive and often assumed without sufficient evidence. But the study of sexual selection involves more than indicators and Fisherian coevolution, as discussed below. We suspect that the book's portrayal of researchers as beholden to the orthodoxy arises, in part, from two distinct ways in which the term "information" is used in the sexual selection and animal communication literature. Prum—and he is not alone—appears to equate information with quality (survival or fecundity value of the signaler), such that any discussion of information is viewed as evidence of indicator thinking. Others, however, use information in a mathematical sense, as in the reduction of uncertainty about a state or attribute, quantified as entropy or bits (Shannon 1948). In this sense, receivers are always detecting, discriminating, and assessing information from signalers, whether it indicates quality or "merely" an aesthetic impression. For example, Prum (2012) asserts that the term "assessment" in mate choice is defined as "cognitive analysis of adaptive information encoded by the signal" and assumes direct benefits or good genes, citing Endler and Basolo (1998). However, the latter article defines assessment simply as "extraction of information" and explicitly discusses how it applies to all models of preference evolution, including Fisherian. Assuming that "information" is equivalent to "indicator value," Prum thus dismisses a article that famously argues for greater consideration of ideas central to aesthetics as just another part of the indicator orthodoxy.

The third problem with this characterization of AMC is that fitness is defined only with respect to viability. The concept of adaptation is even further restricted to mean viability benefits that increase an organism's fit with the "environment" (conspecifics of the opposite sex not included). This definition leads Prum to claim that he and Darwin are the sole champions of nonadaptive mate choice, and that arbitrary mate choice has been "defined out of existence" (p327). The view of Fisherian selection as nonadaptive relies, however, on these restrictive definitions of fitness and adaptation. As noted (p51, p327), modern evolutionary biologists use a broader definition of fitness that includes mating and fertilization success (e.g., attractiveness) as well as viability of both individuals (direct fitness) and their offspring (indirect fitness) (e.g., Kokko et al. 2002; Fuller et al. 2005). This broader definition accounts for the fact that many traits affect reproductive success, either through their effect on survival, fecundity, or mating success; sexually reproducing organisms need all three. Therefore, if a preference for an elaborate male display increases the attractiveness of a female's sons, regardless of whether or how the preference affects her viability, the preference provides an indirect fitness benefit to females (i.e.,"sexy sons"), and her sons enjoy the direct fitness benefit of increased mating success. Calculating fitness this way, Fisherian mate choice is fitness-enhancing and thus adaptive for both sexes, even though displays are arbitrary or detrimental with respect to viability (Kokko 2001). We are not suggesting that Fisherian selection is just another part of the "adaptationist paradigm," but rather that the Fisherian process is not as distinct from adaptive evolution as the book proposes.

Finally, the book's restricted definitions of fitness and adaptation lead to a restricted definition of sexual selection that excludes traits that affect viability, in essence excluding all but late-stage Fisherian and sensory bias models (see below). Prum argues that if sexual selection is defined to include traits affecting both viability and mating success, then it becomes "merely a handmaiden of natural selection (p11)." This value judgment is confusing. More commonly, natural selection is used as an umbrella term for all forms of differential reproductive success, but a distinction is made between sexual selection—differential reproductive success based on competition over mates or fertilization (Andersson 1994)—and viability (ecological) selection, what Darwin referred to as "ordinary" selection—differential reproductive success based on survival and fecundity (Safran et al. 2013; Servedio and Boughman 2017). One is not subservient to the other, nor are they mutually exclusive (see below). Redefining sexual selection to exclude cases where females choose mates based on indicator traits only marginalizes the contribution of sexual selection to evolution.

Darwin's emphasis on aesthetics and his belief that that displays can "serve as a sexual charm, and for no other purpose" is cited in the book as justification for the restricted definition of sexual selection (p26). But not even Darwin explicitly restricted his definition to these cases alone (Darwin 1871; Cronin 1993; Prum 2012). More importantly, it is not clear how this restricted definition advances our understanding of beauty. In all models of sexual selection, with or without viability benefits, "preferences" are subjective, sensory-perceptual-cognitive experiences that can stimulate pleasure, motivate mate choice, and promote beauty in nature. Treating viability benefits and aesthetics as mutually exclusive ignores the possibility that the former is the function of the behavior and the latter is the proximate motivation for it. For example, humans have a preference for fatty and sweet foods because they are energy rich and easily metabolized. The functional benefit of this preference, however, does not diminish the proximate motivation: the subjective, aesthetic joy of eating a perfect cheesecake. Satisfying a desire, whether for cheesecake or a mate, can provide an aesthetic experience, it can be beneficial for viability, or it can be both. There is nothing inherently more aesthetic about the Fisherian model of intersexual selection than alternative models.

The Fisherian Model of Preference-Display Coevolution

Throughout the book, and in previous publications, Prum passionately argues that the Fisherian model of coevolution between female preferences and male displays is the primary (if not the only) cause of beauty in nature (Fisher 1930; see also Prum 2010, 2012). As further developed by Lande (1981) and Kirkpatrick (1982), the model (also called the "L–K" model) quantitatively explores the joint evolution of male sexual displays and female preferences under a scenario in which females can choose among numerous mates, female mate choice is not costly, and males provide only genetic material. It provides a compelling evolutionary hypothesis for the maintenance, spread, and exaggeration of arbitrary displays that need not possess any survival value for the male signaler, female receiver, or their offspring. However, there are several issues with this model as a general explanation of male sexual displays.

AN INAPPROPRIATE NULL

As pointed out by Borgia and Ball (2018), Rosenthal (2017), and others, Fisherian coevolution is not an appropriate null model for the evolution of elaborate displays. In the book, a null hypothesis is described in lay terms as the case when "nothing special" is happening, thus equating Fisherian coevolution with "nothing special." In statistical terms, however, null hypotheses predict the absence of a relationship between variables that are hypothesized to have a causal relationship—i.e., the "alternative" hypothesis. Clearly, the Fisherian model is rife with "special" and, more importantly, testable assumptions and predictions. For example, models of the Fisher process assume that (i) preferences will have a genetic basis (the null is that they do not); (ii) females have mate preferences based on male display traits (the null is random mating); and (iii) genes "for" preferences and genes "for" displays will be in linkage disequilibrium (the null is that they are not) (Lande 1981). Statistically speaking, the Fisherian model contains many testable causal relationships and is therefore an inappropriate null hypothesis.

Viewing Fisherian selection conceptually as a null model of sexual selection—analogous to the Hardy–Weinberg Equilibrium or the Neutral Theory of Molecular Evolution (Kimura 1983)—also fails, because the assumptions underlying the model are not a given across many animal systems. Furthermore, the restrictive nature of the assumptions excludes many reasonable, alternative explanations for the phenomena of interest (i.e., the evolution of beauty), as discussed below. If indicator value of male displays is the hypothesis being tested, then no relationship between signal and mate "quality" is the appropriate null. We appreciate Prum's argument that simply demonstrating such a relationship is insufficient to support AMC, as conclusive evidence requires not just condition-dependence but also a clear fitness benefit for choosers. For example, despite condition-dependent trait expression among displaying males, females of many wolf spider species do not appear to use these traits in mate choice (Shamble et al. 2009; Rosenthal and Hebets 2012; Rosenthal and Hebets 2015). The burden of proof should be on demonstrating indicator value, and we agree that few studies go this far. The solution, however, is not to switch out one set of assumptions for another and accept Fisherian selection by default. Fisherian coevolution is a valid and testable alternative hypothesis for the evolution of beauty, but it is not an appropriate null.

FISHERIAN AND INDICATOR PROCESSES ARE NOT MUTUALLY EXCLUSIVE

A central premise of the book pits Fisherian coevolution against the indicator model, arguing that if the indicator model cannot be supported, then Fisherian must be assumed. This narrow view—and the book's pitting of aesthetic versus utilitarian worldviews—implies that the two models are both mutually exclusive and exhaustive. Alternative hypotheses for display and preference evolution are essentially ignored, and the possibility that both models may be true, or that both may be false, is not seriously considered.

Kokko (2001) and Kokko et al. (2002) note that indicator ("good genes") and Fisherian models are not mutually exclusive, placing these processes on two ends of a continuum. On one end, indicator benefits increase the viability of offspring by the inheritance of the father's "good genes"; on the other, Fisherian ("sexy son") benefits improve the attractiveness of offspring; and in the middle, display traits have some combination of viability and attractiveness benefits for the receiver. Viability and attractiveness are distinguishable benefits, but they may nonetheless work in concert. Viability benefits may favor the evolution of preferences, which could then runaway or evolve more quickly through the Fisher process. The Fisher process also predicts that natural selection will ultimately limit the elaboration of display traits, as tail feathers (for example) cannot be infinitely long. At or near this point, displays can become indicators of male health and condition, which if heritable, may provide additional benefits to choosy females. In other words, displays can originate as indicators and "runaway" through a Fisherian process, or they can originate as arbitrary with respect to viability and ultimately take on an indicator function (Chandler et al. 2013).

Prum (2012) notes that Fisherian traits may become costly or condition-dependent as they become more elaborated, and in some cases, they may become indicators. He reminds us that costliness or condition-dependence alone is not sufficient evidence of viability selection; viability benefits of choosiness much also be demonstrated. As discussed earlier, we agree that this important point is indeed too often forgotten. But it does not follow that one must accept these as Fisherian traits by default until viability benefits are demonstrated, when there are many alternative possibilities (discussed below). Further, the fact that Fisherian traits can become viability indicators highlights the problem of portraying these models as clashing worldviews rather than simply two different, nonmutually exclusive mechanisms by which selection can directly or indirectly favor female preferences. Do preferences favored by viability selection become more aesthetic if they run away by the Fisher process? Do Fisherian traits become less aesthetic if a viability benefit emerges?

FISHERIAN AND INDICATOR PROCESSES ARE NOT EXHAUSTIVE: ALTERNATIVE MODELS

By pitting Fisherian and indicator models against one another—disproving the latter by supporting the former—the book also implies that these two models are exhaustive in explaining the evolution of sexual displays. This is clearly not the case. Sexual displays can evolve through processes not encompassed by this dichotomy.

Male–male competition, for example, is portrayed as a force often opposing aesthetic evolution (p28), but it is a well-supported explanation for many exaggerated secondary sexual traits. The size and noses (and the size of the noses) of elephant seals, the elaborate antlers of elk and other ungulates, and the dazzlingly diverse horns of dung beetles do not appear to be explained by the subjective experiences of females but rather by their role in intrasexual contests (Emlen 2014). Even displays that are not obvious weapons, like nuptial coloration or songs, could arise by intrasexual selection. In darter fish, species-specific male nuptial colors are used in aggressive displays against rival males, and Mendelson et al. (2018) suggest that these colors are exaggerated primarily via intrasexual selection and the aesthetic experiences of males, with female preference arising as a pleiotropic byproduct. In other cases, it may be adaptive for females to assess male intrasexual displays during mate choice because these displays indicate male quality, a process that does not require coevolution of female preferences and displays (Berglund et al. 1996; Borgia and Coleman 2001). Another alternative hypothesis is that elaborate male displays are used in intrasexual contests and females simply prefer the winner, or may be constrained to mate with the winner, with no evolution of female preference for the display itself (e.g., Bradbury and Davies 1987; Wiley and Poston 1996). In all of these cases, intrasexual selection must be considered a plausible alternative to both Fisherian and indicator models of display evolution.

Another set of alternative hypotheses for the evolution of desire and display are the related models of sensory drive (Endler 1992; Endler and Basolo 1998; reviewed in Cummings and Endler 2018) and sensory bias (Basolo 1990a; Ryan and Rand 1993). Sensory drive proposes that displays will reflect the environment in which they are transmitted due to direct effects of the environment on signal propagation and detectability. For example, the Bornean rock frog, *Staurois parvus*, changes the amplitude, pitch, repetition rate, and duration of advertisement call notes in response to noise caused by fast-flowing water (Grafe et al. 2012).

Sensory drive also proposes that sensory and cognitive systems are shaped by an organism's environment over evolutionary time, and that these systems will in turn influence the evolution of display form. Cummings and Endler (2018) recently reviewed the evidence for the environment's role in the evolution of animal sensory capacities and signal form. Relevant to visual beauty, they found strong support for sensory drive processes shaping visual tuning and associated signaling traits (Cummings and Endler 2018). Sensory bias, or preexisting bias, further proposes that adaptations of sensory systems to the tasks of life—feeding, avoiding predators, finding shelter, etc.—will have byproduct effects on sexual signaling and mate choice. In guppy fish, for example, a preference for orange fruits coincides with preference for orange coloration on males (Rodd et al. 2002).

Sensory drive, sensory bias, and related hypotheses of perceptual and processing biases (e.g., Ryan and Cummings 2013) offer critical alternative hypotheses to Fisherian coevolution. For example, preexisting biases can drive divergence in displays without producing a concomitant change in receiver preference (in contrast to Fisherian coevolution), via a process of mutation-order divergence. Mutation-order divergence contrasts with ecological speciation in positing that populations diverge despite inhabiting similar environments, by finding different biological solutions to similar evolutionary problems (e.g., Mani and Clarke 1990). Mendelson et al. (2014) propose that receivers have complex, preexisting preference landscapes such that signalers can be attractive in multiple ways; these preexisting preferences represent the similar environments to which different populations are adapting. Multiple studies demonstrate "hidden," preexisting preferences, that is preference for a broad array of novel displays that do not exist in a receiver's population (reviewed in Ryan 2018). Female platyfish, *Xiphophorus maculatus*, for example, prefer conspecific males with artificial swords attached to their tails despite the absence of swords in natural populations (Basolo 1990b). When a new attractive display element arises by mutation in a geographically isolated population, that population will diverge from its sister as the novel element sweeps to fixation, with potentially no change in receiver preferences across populations. An alternative mutation might arise in the sister population, causing further divergence in beautiful displays, again with no change in "hidden" preferences. Moreover, the novel display element may be more important to male receivers than females, which would rule out a Fisherian process.

Holland and Rice (1998) proposed that initial sensory biases can also lead to the coevolution of traits and preferences, where male displays may evolve to exploit preexisting preferences in females. If this is costly for females, selection may favor a higher threshold for mating (i.e., "resistance"), which may then favor more elaborate displays. This may lead to coevolutionary "chase away" selection, which is similar to a direct benefits model with female preferences selected to reduce costs rather than increase benefits (Kokko et al. 2006).

Finally, in some animal taxa, females have learned mating preferences (reviewed in Vakirtzis 2011; Verzijden et al. 2012; Witte et al. 2015; Varela et al. 2018; Hebets and Sullivan-Beckers, *in press*), likely violating the assumption of a genetic basis for female preferences. In one species of wolf spider (*Schizocosa uetzi*), for example, females are more likely to mate with males that possess a phenotype they have previously experienced; and are simultaneously more likely to cannibalize males of an unfamiliar phenotype (Hebets 2003). Culturally transmitted mating preferences have been identified and explored for decades (Laland 1994; Freeberg et al. 1999; Briggs et al. 1996) and recent studies suggest that learned preferences can work with Fisherian and other types of sexual selection (Bailey and Moore 2012; Verzijden et al. 2012). Even in these cases, however, assuming the conditions of Lande-Kirkpatrick Fisherian selection as a null model would be misleading. Mate choice learning, as well as mutation-order divergence, sensory drive, and bias, sexual conflict, and male–male competition all provide testable nonmutually exclusive alternatives to both Fisherian and indicator models. The two hypotheses contrasted in the book do not represent the sum total of scientific explanations for the evolution and diversification of exaggerated secondary sexual traits.

FISHER IS NOT A GENERAL EXPLANATION FOR BEAUTY OR DESIRE

While Fisherian coevolution may be an important alternative hypothesis, it does not appear to be a powerful general explanation for intersexual selection or beauty more generally. Various models have found that the Fisherian process is weaker in systems where there is direct selection on female preferences—either through a cost to being choosy (Pomiankowski 1987; Pomiankowski et al. 1991) or through stabilizing selection on preferences in other contexts (Fuller et al. 2005). Further, Fisherian models are weak under realistic assumptions about migration rates (Barton and Turelli 1991) and when the mating system is not polygynous (Kirkpatrick et al. 1990). In a particularly compelling example, Fuller et al. (2005) present a simple quantitative genetic model of intersexual selection and simulate each of the major models of sexual selection—including the Fisherian model—and their interactions (see also Kokko et al. 2006). They found that Fisherian selection predominates under a certain set of parameters, but other processes dominate under other conditions. In other words, the Fisherian model is neither a null hypothesis nor ubiquitous; it is a valid alternative hypothesis that best explains beauty only under certain conditions.

Conditions favorable for Fisherian runaway selection are most likely to be met in lekking species, in which females have free, low-cost choice among males and males offer no resources beyond sperm. However, even in lekking systems, the Fisherian model alone may not suffice to explain diversification under many realistic scenarios (Arnold and Houck 2016). Moreover, only a small fraction of animal species with elaborate sexual displays have a lek mating system. For example, in many insect systems, males offer nuptial gifts or nutrients in seminal fluid that provide a clear direct benefit for mate choice (Wagner et al. 2001). In fishes, paternal care is more common than maternal care, even in species with elaborate male displays (e.g., Ridley 1978). In some monogamous birds, females accept or reject males based primarily (or entirely) on the territory or nest site they have secured rather than the male display (e.g., Alatalo et al. 1986). In many systems, direct selection on female preferences will be strong and will constrain Fisherian selection.

Finally, it is worth noting that some of the most flamboyant and diversified displays in the natural world are flowers, which attract pollinators by advertising nectar rewards, through deceptive mimicry, and by tapping into sensory biases. While plant-pollinator coevolution is offered as an example of aesthetic evolution (p120), the argument that Fisherian selection is critical in the evolution of beauty is undermined by these beautiful and complex displays in systems where Fisherian coevolution is impossible. In sum, Fisherian coevolution is likely an important force in sexual selection, but the diversity of elaborate signals in systems where Fisherian selection is expected to be weak or absent, as well as in systems where viability benefits are clear, undermine the book's central assertion that Fisherian selection is singularly powerful in explaining the dramatic elaboration and diversity of nature's beauty.

Multimodal Communication and Preference Evolution

As researchers interested in the evolution of complex (and often beautiful) sexual displays and associated preferences, we were particularly disappointed by the book's rejection of multimodal communication research as a means for understanding the evolution of beauty. The field, which addresses why signals often involve multiple components and sensory modalities, is curtly dismissed as "an attempt to flatten aesthetic complexity into a manageable set of individualized, rational utilities" (p79).

Our view of this field is quite different. Not only is multimodal signaling directly relevant to understanding the evolution of beauty in animal displays, but it can provide unique insights into the mechanisms driving desire. In direct contrast to the book's assertion, much of multimodal signaling research explicitly aims to expand beyond indicators by integrating aesthetic complexity into the study of communication. A primary focus of this subfield is the interactive and synergistic effects of sensory integration and their influence on receiver response (Patricelli et al. 2003; Hebets 2005; Hebets and Papaj 2005; Rosenthal and Hebets 2012; Taylor and Ryan 2013; Rosenthal et al. 2018)—just the opposite of "individualized utilities." Moreover, many hypotheses explaining the function of multimodal signaling are agnostic with respect to the indicator value of signals and are fully consistent with the notion of arbitrary signals (Hebets and Papaj 2005). For example, display components that alert a receiver to another component can have no hypothesized "meaning" themselves (see Alerting and attention-altering; Hebets and Papaj 2005). Finally, the perception of "beauty" can be intensified through the integration of multiple modalities, making multimodal signaling particularly relevant for understanding the evolution of elaborate, multicomponent displays. In a book that argues for a scientific approach to beauty, it is ironic that a field of behavioral research explicitly dedicated to that aim is dismissed out of hand.

Birds and Bedbugs Make Bad Politics

Finally, we offer a critical reminder that the behavior of nonhuman animals, sexual or otherwise, cannot and should not be used as a moral compass for our own lives. The book explicitly uses "sexual autonomy" in birds to support feminism in humans (see pp. 177–178). As previously pointed out by Borgia and Ball (2018), not only does this argument commit the naturalistic fallacy, but it opens the door to the justification and rationalization of other common, arguably undesirable, behavior. Lions and coots, for example, are notorious child killers; cuckoldry is relatively common in birds; male bed bugs traumatically inseminate females by injecting sperm into their abdomens; and numerous insects and arachnids engage in coercive mating or sexual cannibalism. Indeed, male self-sacrifice and subsequent sexual cannibalism has evolved in multiple spider species, but we suspect no man would use this as a justification to encourage such behavior in humans.

The examples of bird sexual autonomy highlighted throughout the book are evolved phenomena resulting from millions of years of selection on individuals. By comparison, the choice to treat men and women equally is a rational, moral decision for the good of individuals and society. Resting our politics and morality on what we see other animals do is the real "dangerous idea" here. Despite the book's narrow taxonomic worldview (restricted to birds), animals and their sexual behavior are tremendously diverse, each with their own unique evolutionary history. Indeed, it is this diversity that personally drew each of us to the study of sexual selection. Within this diversity, humans could find justification for almost any behavior. Using nonhuman animals as our moral compass would be not only devastating to our society but would also bias our scientific approach to the study of nature.

Along these lines, one of the most outrageous claims in the book is that because "some core, fundamental commitments of eugenics were 'baked into' the intellectual structure of evolutionary biology" (p326), researchers who support a hypothesis of adaptive mate choice fall in lock step with Nazi sympathizers and other eugenicists who promoted sexual reproduction only among humans with high viability traits (Fisher prominent among them; Fisher 1915, 1930). The book argues that "aesthetic evolution provides an essential antidote to this poisonous intellectual history" (p326) and suggests that the acceptance of Fisherian mate choice can not only save biologists from the blind acceptance of a flawed hypothesis, but can also save the world from the evils of human eugenics (pp. 329–330). The effectiveness of this antidote is questionable, given that the very book in which Fisher proposes his theory of sexual selection also dedicates five chapters to human eugenics (Fisher 1930). Moreover, would the Nazi preference for blonde hair and blue eyes have been any less morally repugnant if it had been based explicitly on aesthetics rather than on a misguided belief that these traits also had indicator value? The moral peril arises from the forceful removal of reproductive freedom by those in power, not from dissecting the selective pressures driving mate choice in birds. These arguments are reminiscent of those who urge us to abandon teaching natural selection in schools because of its historical misuse by Social Darwinists. By this logic, any discussion of the genetic basis of traits related to health, even in biomedical research, would be morally wrong. While we cannot let the past misuse of evolutionary theory constrain our current and future research, biologists— regardless of their view of Fisherian sexual selection—should remember the legacy of eugenics and guard against the misuse of science for political power. The truly dangerous idea in this book—applying the lessons of natural selection to our own politics and morality—however, hinders rather than helps that goal.

Conclusion

If the book's main goal is to explain the evolutionary origin of "beauty," as it seems to be, it falls short in numerous ways. The book's central argument is that indicator models have been accepted without evidence and that Fisherian selection has been defined out of existence. Ironically, it proposes that we instead accept Fisherian selection without evidence and redefine sexual selection to explicitly exclude adaptive mate choice. This does not advance our understanding of mate choice or aesthetics. Nor does creating a false dichotomy between adaptation and aesthetics, assuming that beauty only arises from coevolving female preferences, and dismissing or ignoring decades of research on receiver psychology. The book also unfairly caricatures most sexual selection researchers as not only failing to acknowledge the subjective experiences of nonhuman animals, but also of supporting human eugenics and antifeminist politics. Moreover, by arguing that beauty is "irrational," "unpredictable," and simply "happens," the book seems to simultaneously argue for the scientific study of beauty while setting it outside the bounds of scientific understanding.

Two new books on beauty, desire, and the evolution of elaborate displays offer different perspectives on this field. Mike Ryan's "*A Taste for the Beautiful—The Evolution of Attraction*" (2018) picks up where *The Evolution of Beauty*" leaves off. Ryan explicitly asks how aesthetic preferences are formed, exploring how beauty and desire are defined in the brains of receivers. Gil Rosenthal's "*MATE CHOICE–The Evolution of Sexual Decision Making from Microbes to Humans*" (2017) encompasses a broader range of both topics and organisms, touching on many of the same conversation points as *The Evolution of Beauty*. Indeed, Rosenthal also challenges the "conventional view" that females choose mates for their viability benefits, synthesizing research from a range of distinct disciplines (e.g., animal behavior, neuroscience, economics) to support his claims. Though potentially less accessible to a nonscientific audience, Rosenthal's book provides a more complete and balanced portrayal of the modern science of beauty and desire.

Finally, despite numerous concerns, we applaud the passionate descriptions of nature's beauty throughout the book. Prum's enthusiasm for the study of sexual selection and ornithology is infectious. As evidenced by its nomination for a Pulitzer Prize in nonfiction, it has been successful in increasing the public's interest in, and excitement for, science and nature. The book also succeeds portraying a diverse set of scientists as relatable, an important goal of science communication as it can build trust between scientists and the public (Hebets 2018). Furthermore, if the book's effect on evolutionary biology and behavioral ecology is to rattle potentially entrenched assumptions, to raise the bar for evidence of indicator value, to encourage a more thorough consideration of the possibility that displays are arbitrary, or to motivate new statistical tests of arbitrary mate choice (e.g., equivalence tests, Rose et al. 2018), then its publication will undoubtedly have a positive impact on scientific progress. Moreover, we appreciate the focus on beauty and aesthetics, as we agree that there is great promise in exploring the relatively untapped interface between evolutionary biology and the psychology and philosophy of art and aesthetics.

AUTHOR CONTRIBUTIONS

All authors contributed equally to drafting and editing this work.

ACKNOWLEDGMENTS

We are grateful for stimulating conversations with R. Prum, which inspired us to question our assumptions, and inspired further insightful conversations and debates about beauty and aesthetics with G. Arnqvist, P. Brennan, C. Clark, H. Copeland, J. Coyne, M. Cummings, E. DuVal, D. Emlen, L. Fusani, M. Hauber, D. Kikuchi, M. Kirkpatrick, J. Price, T. Price, G. Rosenthal, M. Schmidt, E. Svensson, M. Turelli, and members of our labs. We are also grateful to J. Coyne for insightful comments on a manuscript draft. We thank the NYU Wondercabinet and Ettore Majorana Foundation and Centre for Scientific Culture for sponsoring conferences focused on the evolution of aesthetics.

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